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Research article

Leaf traits and foliar herbivory in tropical dry evergreen forest of India

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Abstract: We investigated leaf traits of 110 plant species and the seasonal patterns of leaf damage by diverse foliar herbivores in tropical dry evergreen forest (TDEF) on the Coromandel Coast of India. The leaves of 110 plant species of TDEF are consumed by fifty-four species of foliar herbivores that includes beetles, larvae and grasshoppers. Mean leaf damage ranged from 1.8% to 21% during the study period (2012–14). The mean leaf damage varied by season with a high value of 16.19±10.44% in monsoon, 9.66±6.66 % in pre-monsoon, 5.24±4.10 % in post-monsoon and 1.97±1.52 % in summer. Among tree species, *Memecylon umbellatum* showed maximum leaf damage and among liana species, *Combretum albidum* suffered maximum leaf damage. Information on different leaf resource users and their food-plants provide an insight into the complex web of forest biotic interactions and such data will be valuable for biological conservation.

Keywords: Foliar herbivores - Leaf damage - Leaf traits - Seasonal variation - Tropical dry evergreen forest.

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INTRODUCTION

Herbivory among plant species can greatly affect the functioning of forest ecosystems (Schuldt *et al.* 2012) and might play an important role in structuring tropical forests (Wright 2007, Viola *et al.* 2010). Different studies found that herbivory differed among species (Barone 1998, Marquis *et al.* 2001, Xiang & Chen 2004, Unsicker & Mody 2005) and was associated to various leaf traits (Marquis *et al*. 2001, Forkner *et al*. 2004, Xiang & Chen 2004). Plants have the capacity to resist or tolerate the foliar herbivory and they can show large differences in the rate of damage by differing their leaf traits (Loranger *et al.* 2012). According to Belsky (1986) herbivory benefits certain plant species by increasing their net primary productivity and seed production by removing senescent tissue and these changes increase plant fitness and supports the herbivore-plant mutualism. Leaf herbivory induces changes in leaf defensive compounds (Karban & Baldwin 1997) and that can affect pollination by inducing nectar defensive compounds (Adler *et al.* 2006). Recent analysis indicates that secondary metabolites are of less importance as a defence against herbivory than morphological and life-history traits (Carmona *et al.* 2011). A positive relationship between the rate of insect herbivory and plant diversity was also documented in subtropical forests of south-east China (Schuldt *et al.* 2010). To understand the effect of foliar herbivores on plant species, it is essential to quantify the variation in the rate of leaf damage and the preference of insect herbivores that affect the foliage of those plants (Marquis 1991, Cuevas-Ryes *et al.* 2006).

The level of insect herbivory is generally lower than most vertebrate herbivory, because structural barriers that are insignificant to vertebrates may be significant to insects (Peeters 2002). Therefore leaf traits including surface, textures, anatomy and morphology have the capacity to block insect feeding. Hoffman & McEvoy (1985) held that 'trichomes' in leaf surface prevent the feeding of leaves by some sucking insects, but not for other herbivores. Leaves containing waxes and thick cuticle on their surface also protect them from insect herbivory (Edwards 1982, Potter & Kimmerer 1988). Leaf texture is an important trait of plant species that plays a major role in plant-herbivore interaction (Peeters 2002).

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The relationship between local host plant and their foliar herbivores have been studied in different tropical forests (Janzen 1988, Marquis 1991, Basset 1991, Basset 1992, Barone 1998). Host specificity of herbivores is frequently characterised by the distribution of herbivore densities throughout a set of local plant species (Novotny *et al*. 2003). Host-plant interaction is an important ecological characteristic of herbivore species as it determines their resource base and acts as a key factor in regulating their density and their relation with other herbivores (Novotny 2002).

The impact and patterns of leaf damage of foliar herbivores have been documented in a few tropical forests (Coley 1980, Janzen 1981, Cruz & Dirzo 1987, Coley & Baron 1996) and poorly documented in tropical dry forest (Janzen 1981, Filip *et al.* 1995). Recent studies suggest that the top-down effects of plant resource users are integral to the structure and functioning of ecosystem (Duffy 2002). No information is available on foliar herbivory in tropical dry evergreen forest vegetation and hence the present study was undertaken with an objective of investigating leaf traits and foliar herbivory and their relationship with respect to season. Here, we assessed leaf traits, and diversity of foliar herbivores, the extent of leaf damage across various seasons and the relationship between them in tropical dry evergreen forest (TDEF) on the Coromandel Coast of peninsular India. In this study we addressed the following questions (1) Does the foliar herbivory in tropical dry evergreen forest differ with season? (2) How variable are the leaf traits of TDEF plant species and (3) to check whether the leaf traits had significant influence on the extent of leaf damage in the studied forest?

MATERIAL AND METHODS

Study area

This study was conducted in tropical dry evergreen forest located in Villupuram (11°56′ N and 79°53′ E) and Cuddalore (11°43′ N and 79°49′ E) districts of Tamil Nadu on the Coromandel Coast of peninsular India. For the present study, we selected a total of nine tropical dry evergreen forest sites, as to cover all plant species of TDEF. Site Puthupet (PP- 12°03′ N and 79°52′ E), Oorani (OR- 12°09′ N and 79°52′ E) and Vada Agaram (VA- 72°10′ N and 79°55′ E) are located respectively 15, 28 and 32 km north of Puducherry town (11°56′ N and 79°53′ E) and six other sites Kuzhandhaikuppam (KK- 11°43′ N and 79°38′ E), Thirumanikkuzhi (TM- 11°43′ N and 79° 41′ E), Suriyanpet (SR- 11°44′ N and 79°38′ E), Sendhirakillai (SK- 11°30′ N and 79°41′ E), Palvathunnan (PT-11°32′ N and 79°41′ E) and Kothattai (KT- 11°30′ N and 79°42′ E) are located 45 to 50 km surrounding of Puducherry town. The forest area of each study site ranges from 1.2 to 10 ha. Fifty-year (1954 to 2014) climate data of the nine sites revealed a mean annual temperature of 28.3 ºC and the mean annual rainfall of 1,171 mm (Parthasarathy 2015). The mean number of rainy days in the annual cycle is 55.5. The climate is tropical dissymmetric type with the bulk of the rainfall received during the northeast monsoon (October–December). Soils are red ferralitic belonging to the Cuddalore sandstone formation of the Miocene period (Meher-Homji 1974). The vegetation of this area is tropical dry evergreen forest type. These closed-canopy forests are 2–3 layered, tree-dominated and liana-dense (Champion & Seth 1968, Parthasarathy *et al.* 2008). The canopy is about 10–12 m in height, dominated by large trees such as *Pterospermum canescens* and *Lannea coromandelica*, while the sub-canopy is composed of smaller trees such as *Memecylon umbellatum*, *Canthium dicoccum* and *Garcinia spicata.* Major lianas include *Strychnos lenticellata* Dennst., *Combretum albidum* G. Don., *Reissantia indica* (Willd.) Halle, *Pyrenacantha volubilis* Wight and *Capparis zeylanica* L. *Ecbolium viride* (Forsskal) Alston and *Sansevieria roxburghiana* Schultes & Schultes f. are the major native perennial herbs present in this forest type (Parthasarathy *et al.* 2008).

Study design

Leaf traits and per cent leaf damage were studied from August 2012 to July 2014 by sampling a total of 13,200 (30 leaves × 110 plant species × 4 seasons) leaves from 606 individuals of 110 plant species (60 trees, 45 lianas and 5 herbs) of tropical dry evergreen forest along with their leaf-eaters (Appendix I). Over the study period, per cent leaf damage was recorded four-times in a year. We classified each year into four seasons such as monsoon (October–December), post-monsoon (January–March), summer (April–June) and pre-monsoon (July–September) on the basis rainfall data (Selwyn & Parthasarathy 2006, Parthasarathy *et al.* 2015). A minimum of 2 to 4 individuals for each species (for rare and sub-dominant species) to a maximum of 10 individuals (for common and dominant species) were sampled to evaluate leaf traits and foliar herbivores. Thirty leaves were collected from each plant species and calculated the per cent of leaf damage by mapping on graph sheet. Foliar herbivore damage was estimated as: folivory (%) = (total leaf area – remnant leaf area / total leaf area) × 100. Leaf traits studied include leaf type, texture, surface, size and specific leaf area (SLA). Besides our observations, relevant literature and regional flora books (Gamble & Fisher 1915–1935, Matthew 1991) were referred to confirm the categorization of leaf traits (Appendix I).

Foliar herbivores of each species were observed for a minimum of one day (06.00–18.00 hrs.) during the study period with the aid of binocular and captured in digital camera. Leaf twig was carefully pushed inside a polythene bag and then clipped with the insects feeding on them (except lepidopteran larvae). Insects were reared on appropriate plant materials until their host status could be confirmed or until they reached the adult stage. We taxonomically identified the collected foliar herbivores of each plant species and the collected lepidopteran larvae were reared in the laboratory until the emergence of adult insects, which were later identified and un-identified larvae classified as morpho-species. Insects that were reared to adult or that died in the process of rearing and confirming their feeding habits were preserved by either pinning (for adult specimen) or in alcohol (for larvae and beetles). One-way ANOVA was used to determine whether leaf damage and leaf traits (type, texture, surface, leaf area) significantly differed among species or seasons sampled.

RESULTS

Foliar Herbivory Across Various Seasons

The mean leaf damage by foliar herbivores ranged from 1.8% to 21% (with an overall mean of 8.3%) for the assessed 13,200 leaves from 606 individuals of the 110 plant species during two-year study period. In the four seasons studied, the mean leaf damage was maximum (16.19±10.44%) in monsoon followed by pre-monsoon (9.66±6.66%), intermediate in post-monsoon (5.24±4.10%) and least (1.97±1.52 %) in summer (Table 1). Per cent leaf damage differed significantly across the four seasons (F = 96.52, P < 0.05) in TDEF. Plant species displayed differences in leaf damage: among tree species *Memecylon umbellatum* (with 21% of mean leaf damage), *Canthium dicoccum* (19%) and *Lepisanthes tetraphylla* (18%) showed higher levels of leaf damage. Among liana species, *Combretum albidum* (15%), *Reissantia indica* (14%), and *Cissus vitiginea* (13%) had higher levels of folivory.

Table 1. Seasonal patterns of foliar herbivory in tropical dry evergreen forest on the Coromandel Coast of India. Values are monthly average for the study period (August 2012-July 2014).

% leaf damage	Monsoon	Post-monsoon	Summer	Pre-monsoon
2012-13	16.16 ± 10.35	5.12 ± 3.99	1.94 ± 1.46	9.51 ± 6.59
2013-14	17.01 ± 10.76	5.57 ± 4.34	2.09 ± 1.62	10.20 ± 7.04
Total (mean)	16.19 ± 10.44	5.24 ± 4.10	1.97 ± 1.52	9.66 ± 6.66

Leaf traits and foliar herbivores

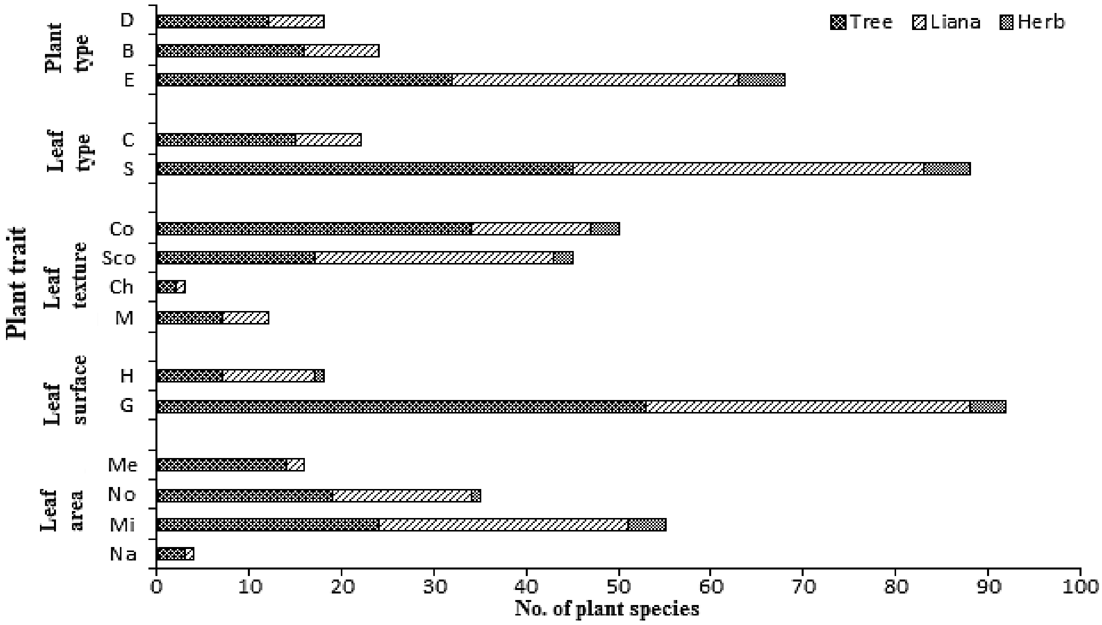

Figure 1. No. of plant species of different life-forms (tree, liana, herb) with respect to leaf traits of a total of 110 plant species in tropical dry evergreen forest on the Coromandel Coast of India (for expansion of codes see Appendix I).

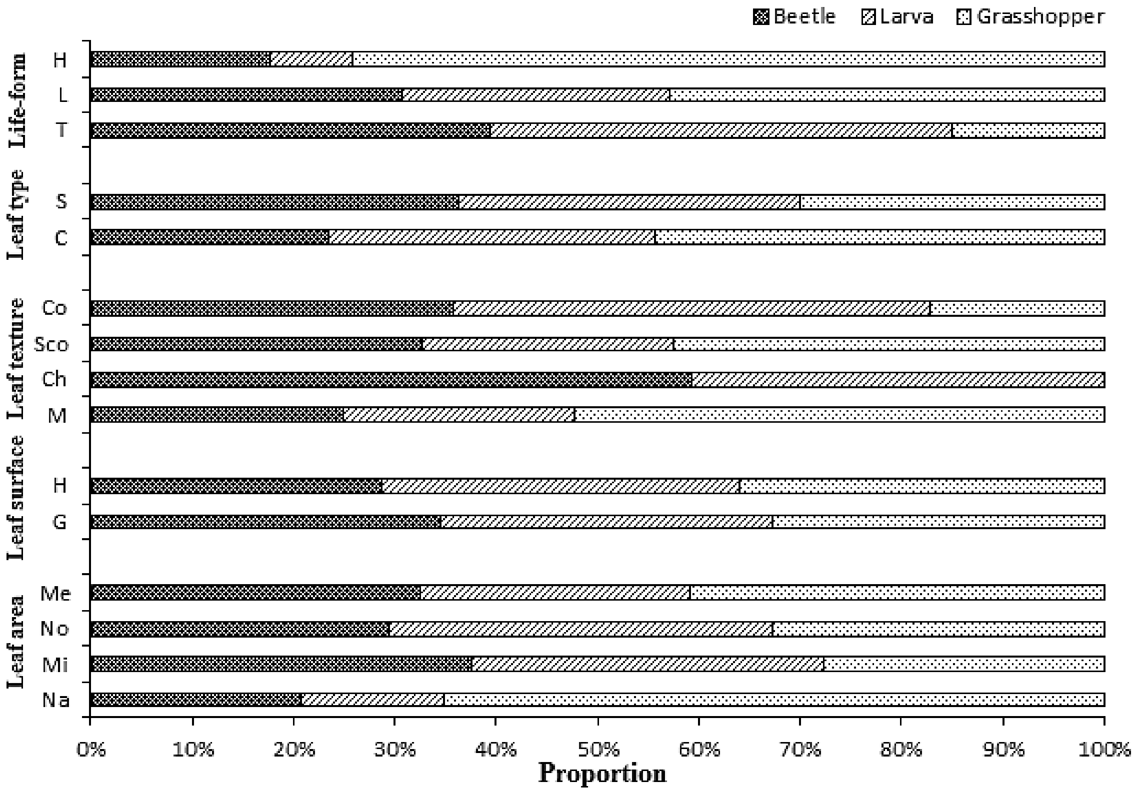

Figure 2. Proportion of plant species with respect to foliar herbivory among various leaf traits of tropical dry evergreen forest (for expansion of codes sees Appendix I).

In tropical dry evergreen forest, eighty per cent of plant species have simple leaves and just 20% have compound leaves (Fig. 1). The coriaceous leaf texture (45%) was common followed by sub-coriaceous (41%) membranous (11%) and chartaceous (3%) category. The glabrous leaf surface was common (84%) and just 16% of species have 'hairy' leaves. In leaf area, microphyll dominated (50%) followed by notophyll (32%), mesophyll (14%) and nanophyll (4%). Beetles and lepidopteran larvae were the dominant leaf-eaters in TDEF, followed by grasshoppers (Fig. 2) and their details are dealt by groups: Beetles (Fig. 3B & J) - Eight species of beetles consumed leaves of 63 plant species (57%) in TDEF. Among the total 110 plant species, fifty-eight species are exclusively folivored by beetle species (Table 2). Beetles utilised leaves of both trees (52%) and

Table 3. List of foliar herbivores (common name, scientific name for identified species, and faunal code) that utilise leaves of one or many of the 110 plant species in tropical dry evergreen forest on the Coromandel Coast of India.

Foliar herbivore	Code	Foliar herbivore	Code
Lepidopteran larvae (38 plant species were exclusively utilised)			
Moth larva 1	L1	Moth larva 21	L21
Moth larva 2	L2	Moth larva 22	L22
Moth larva 3	L3	Moth larva 23	L23
Moth larva 4	L4	Moth larva 24	L24
Moth larva 5	L5	Moth larva 25	L25
Moth larva 6	L6	Moth larva 26	L26
Moth larva 7	L7	Moth larva 27	L27
Moth larva 8	L8	Moth larva 28	L28
Moth larva 9	L9	Angled castor (*Ariadne ariadne)*	L29
Moth larva 10	L10	Yellow orange tip (*Ixias pyrene)*	L30
Moth larva 11	L11	Common grass yellow (*Eurema hecabe)*	L31
Moth larva 12	L12	Indian common Mormon (*Papilio polytes)*	L32
Moth larva 13	L13	Lemon pansy (*Junonia lemonias)*	L33
Moth larva 14	L14	Lemon emigrant (*Catopsilia pomona)*	L34

Moth larva 15	L15	Mottled emigrant (*Catopsilia pyranthe)*	L35
Moth larva 16	L16	Painted hand maiden moth (*Euchromia polymena)*	L36
Moth larva 17	L17	*(Papilio* sp.)	L37
Moth larva 18	L18	Plain tiger larva (*Danus chrysippus)*	L38
Moth larva 19	L19	Tawny coster (*Acraea violae)*	L39
Moth larva 20	L20		
Beetles (58 plant species utilised exclusively)			
Unknown	Bt1	Jewel beetle (*Sternocera chrysis)*	Bt5
Leaf beetle (*Chrysochus auratus)*	Bt2	June beetle (*Phyllophaga* sp.)	Bt6
Unknown	Bt3	Net winged beetle (*Lycostomus praeustus)*	Bt7
Unknown	Bt4	Flower beetle (*Clinteria coerulea)*	Bt8
Weevils			
Straight-snouted weevil (*Rhopalapion longirostre)*	W1	Leaf rolling weevil (*Apoderus scutellaris)*	W2
Grasshoppers (4 plant species utilised exclusively)			
Unknown	Gh1	*Melanoplus* sp.	Gh4
Unknown	Gh2	Hooded grasshopper (*Teratodes monticollis)*	Gh5
Unknown	Gh3		

lianas (43%) in closer proportion. They chose largely simple leaf type (84%) with glabrous surface (84%), sub-coriaceous (46%) and coriaceous (41%) leaf texture followed by membranous (9%) and chartaceous (3%) category. With regard to leaf size, microphyll (54%) leaves are largely utilised by beetles followed by notophyll (27%), mesophyll (15%) and nanophyll (3%). Larvae (Fig. 3D, F, G, I, K & L) - In TDEF, 29 different morpho-species of lepidopteran larvae used leaves of 46 plant species (42%) as food source and largely preferred leaves of lianas (61%) over tree species (37%). Leaves of thirty-eight plant species in TDEF are exclusively consumed by lepidopteran larvae (Table 2). Like the other foliar herbivores (beetles, grasshoppers) lepidopteran larvae mainly fed upon 'simple' leaves (78%) with coriaceous (54%) and sub-coriaceous textures (35%). Grasshoppers (Fig. 3C) - Five species of grasshoppers utilised leaves of 10 plant species (9%) of which four species are exclusively fed upon by them (Table 2) in TDEF and majority of them chose leaves of lianas (60%). Grasshoppers consumed leaves of sub-coriaceous (60%), coriaceous (20%) and membranous (20%) texture, simple leaves (70%) with glabrous surface (80%) and microphyll (40%) leaf size.

Variation in leaf traits and per cent leaf damage

A significant relationship exists between per cent leaf damage and various leaf traits (Table 3). In tropical dry evergreen forest, leaves of tree species are consumed more than those of liana species and the leaf damage was significantly related during pre-monsoon (F = 10.06, P < 0.05) and post-monsoon season (F = 4.0, P < 0.05). Tree species exhibit high mean leaf damage in post-monsoon (6.41±4.86) and pre-monsoon (2.25±1.82) seasons than those of liana species. Among tree species, *Ficus hispida* (19.3%) suffered maximum leaf damage in post-monsoon and *Memecylon umbellatum* (39%) in pre-monsoon season. One-way ANOVA revealed that there was no relationship between plant physiognomic type and per cent leaf damage (P > 0.05), so also between leaf surface and per cent leaf damage. Leaf texture was significantly related to leaf damage in monsoon season (F = 3.25, P < 0.05). Species with coriaceous leaf texture suffered high mean leaf damage (19.04±10.96) in monsoon season than those of sub-coriaceous (15.95±10.22), membranous (8.92±5.71) and chartaceous texture (18±9.26). Coriaceous leaves of *Memecylon umbellatum* recorded maximum leaf damage (43%) and membranous leaves of *Abrus precatorius* had minimum leaf damage (2%) in monsoon season. Results of one-way ANOVA revealed a higher level of significance between leaf area and per cent leaf damage during post-monsoon (F = 17.36, P < 0.05) and summer (F = 12.06, P < 0.05). Mesophyll leaves were consumed largely in post-monsoon (10.86±3.35) and summer (3.76±1.73) season. Mesophyll leaves of *Ficus hispida* (19.23) recorded maximum leaf damage and nanophyll leaves of *Abrus precatorius* (0.23%) exhibit minimum leaf damage in post-monsoon season also. In summer, notophyll leaves of *Cassia fistula* (7.32%) are largely consumed by foliar herbivores (Appendix I).

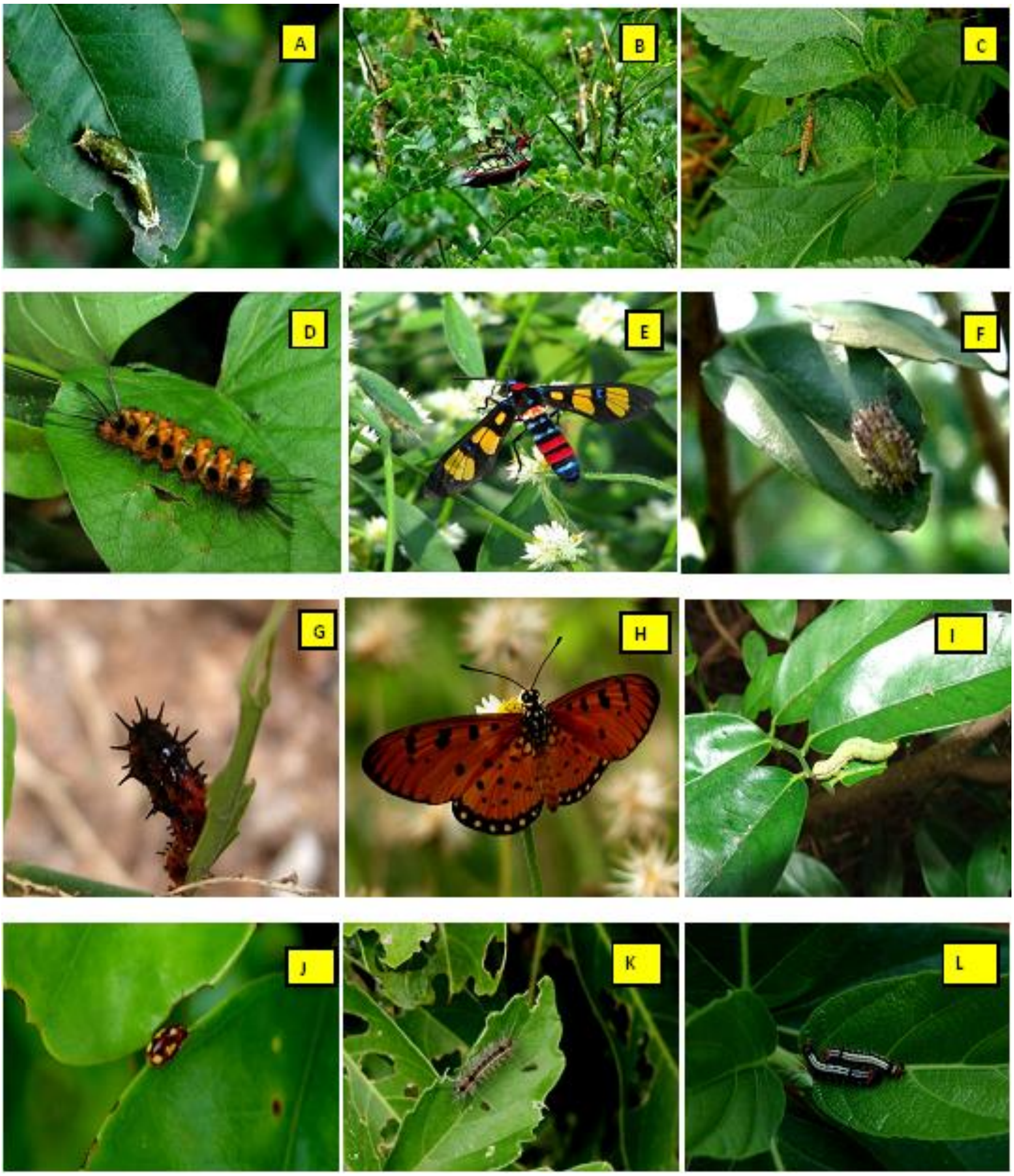

Figure 3. Various foliar herbivores (beetle, larvae, and grasshoppers) utilized different plant life-forms in tropical dry evergreen forest on the Coromandel Coast of peninsular India; **A,** Larva on coriaceous leaves of *Atlantia monophylla*; **B,** Jewel beetle in membranous leaves of *Acacia caesia*; **C,** Grass hopper in sub-coriaceous leaves of *Lantana camara*; **D,** Painted hand maiden moth larva in *Argyreia cymosa*; **E,** reared adult of Painted hand maiden moth larva; **F,** Moth larvae in *Memecylon umbellatum*; **G,** Larvae of Tawny coster feeding leaves of *Ecbolium viride*; **H,** Reared adult of Tawny coster larva; **I,** Larva in *Diospyros ebenum*; **J,** Beetle folivored notophyll leaves of *Canthium dicoccum*; **K,** Moth larva in microphyll leaves of *Cayratia pedeta* and **L,** Moth larva in mesophyll leaves of *Ficus hispida*.

DISCUSSION

Foliar herbivory across various seasons

Our study documented the per cent of leaf damage caused by foliar herbivores in tropical dry evergreen forest (TDEF) on the Coromandel Coast of peninsular India. In general, the mean annual per cent of leaf damage in tropical dry evergreen forest is higher than temperate forest (7.1%) and lower than other tropical wet evergreen forest (11.1%) as reported in various tropical forests by Coley & Aide (1991). Leaf damage averages 8.3% for 110 plant species of TDEF on the Coromandel Coast of India, and this is about one and a half fold greater (14.9%) than that of 37 tree species of Chamela-Cuixmala biosphere reserve in Mexico (Cuevas-Reyes *et al.* 2006) and almost double (16%) in Luquillo experimental forest on Puerto Rico for the 8 tree species studied. In lowland tropical forest, mean per cent folivory ranged from 7 to 20.3 % (Coley & Aide 1991), but in TDEF the variation was 1.8% to 21% for the studied 110 plant species. This may be because our study was conducted on adult plants of different life-forms (60 trees, 45 lianas, 5 herbs), while Coley's study mainly focussed on saplings of trees, where leaf damage is generally high (Coley & Barone 1996).

Table 3. Per cent leaf damage in four seasons with respect to leaf traits in tropical dry evergreen forest on the Coromandel Coast of India. One- way ANOVA showed significant variation among various leaf traits ($P < 0.05$).

Plant traits		Monsoon			Post-monsoon			Summer			Pre- monsoon		
		Mean±Sd	***F***	***P***	**Mean±Sd**	***F***	***P***	**Mean±Sd**	***F***	***P***	**Mean±Sd**	***F***	***P***
Life-form	T	18.20±10.45	3.38	0.06	6.41±4.86	10.06	**0.00**	2.25±1.82	3.51	0.06	10.97±6.89	4.00	**0.04**
	L	14.43±10.27			3.92±2.28			1.69±0.95			8.36±6.24		
Plant type	E	15.62±10.58	0.80	0.44	4.99±3.68	1.54	0.21	1.96±1.42	0.54	0.58	9.44±7.21	0.38	0.68
	B	18.77±10.31			5.11±4.61			1.89±1.66			10.84±5.59		
	D	17.06±10.54			6.89±4.86			2.35±1.74			9.99±6.47		
Leaf type	C	15.80±10.54	0.15	0.69	4.74±4.16	0.58	0.44	1.76±1.74	0.75	0.38	10.41±6.43	0.19	0.66
	S	16.80±10.54			5.50±4.14			2.08±1.47			9.71±6.82		
Texture	M	8.92±5.71	3.25	**0.02**	4.67±4.08	0.98	0.40	1.63±1.54	0.37	0.771	6.22±4.12	2.02	0.11
	Ch	18±9.26			8.21±3.25			2.33±1.15			12.07±5.71		
	Sc	15.95±10.22			4.83±3.58			1.97±1.41			9.29±6.45		
	Co	19.04±10.96			5.79±4.63			2.12±1.67			11.15±7.26		
Surface	G	16.75±10.52	0.09	0.75	4.99±3.57	2.97	0.08	2.03±1.52	0.05	0.81	9.92±6.95	0.04	0.83
	H	15.96±10.63			6.68±5.71			1.94±1.60			9.59±5.90		
Leaf area	Na	8.27±9.76	1.64	0.18	1.55±1.37	17.36	**0.00**	0.58±0.41	12.06	**0.00**	6.46±5.71	1.46	0.23
	Mi	15.48±10.66			4.54±4.17			1.63±1.31			8.94±7.35		
	No	18.95±10.20			4.39±1.99			1.93±1.20			11.63±6.10		
	Me	17.15±10.04			10.86±3.35			3.76±1.73			9.83±5.58		

Note: For expansion of codes see Appendix 1.

Leaf traits and foliar herbivores

Leaves of tropical dry evergreen forest are fed upon by diverse foliar herbivore groups such as Coleoptera, Lepidopteran larva and Orthoptera and these foliar herbivores are also the most important leaf eaters in various other tropical forests (Angulo-Sandoval & Aide 2000, Arnold & Asquith 2002, Williams-Linera & Herrera 2003, Angulo-Sandoval *et al*. 2004, Mazia *et al*. 2012). Coleopterans are the major leaf-eaters (of 57% plant species) in tropical dry evergreen forest as also reported in many other tropical forests (Murali & Sukumar 1993, Varanda & Paise 2006). In our study, leaves of more than 50% of plant families are consumed by a single faunal group and this pattern of leaf damage suggests that specialist foliar herbivores are more important than generalists and it supports the assumption of Janzen-Connell model (Janzen 1970). The leaf damage caused by twenty-nine species of Lepidopteran larvae exhibited a high degree of specialisation in TDEF and that is not the case with beetles and grasshoppers. Arnold & Asquith (2002) also reported high diversity and density of Lepidopteran larvae in the fragmented forest of Lago Gatun, Panama. The leaf damage of 38 plant species was caused by 29 morpho-species of specialist larval herbivores in TDEF. This result suggests that specialist insect herbivores are more important than generalist herbivores and this observation corroborates with the global pattern of lepidopteran specialist feeders (Scriber 1973).

A noticeable trend in this study is the peak of insect abundance during the monsoon and pre-monsoon seasons and this account for maximum leaf damage in these seasons. According to Coley & Barone (1996), foliar herbivore populations are less during dry season, with a marked increase at the beginning of wet season and the concordant rates of herbivory being lowest in the dry season and highest in rainy season. The higher leaf damage in monsoon and pre-monsoon season in TDEF is probably due to the activity of Lepidoptera larvae, which are more abundant in these seasons. Evidence from the literature (Raffa *et al.* 1992, Mopper & Simberloff 1995) provides a possible explanation that foliar herbivores respond to seasonal variation in food resources by contemporizing their life-cycle with the phenology of their host plant species and in our observation most of the plant species in TDEF show a peak in leaf-flushing during pre-monsoon and monsoon seasons. Lowman (1992) also reported a higher level of leaf damage during the peaks of leaf production. Angulo-Sandoval & Aide (2000) reported that when leaf production decreases an increase in predator density of foliar herbivores will reduce the herbivore density and that could be the possible reason for less leaf damage in TDEF also during the post-monsoon and summer seasons.

Variation in leaf traits and per cent leaf damage

In the present study, tree species are highly folivored than liana species because liana leaves are more exposed to sun and the level of herbivory in canopy usually less than the leaves at sub-canopy and understory levels as also reported from the sub-tropical and temperate rain forest of New South Wales (Lowman 1985). This study found that the extent of insect herbivory varied significantly with leaf traits and season (Table 1 & 3). Overall, coriaceous and sub-coriaceous textures of leaves in tropical dry evergreen forest (TDEF) can be considered as palatability enhancers to the foliar herbivores and this result also agrees with Lu & Lee (2010) who found that leaf traits may play a key role in the host choice of foliar herbivores and the extent of leaf damage. Our results also suggest that foliar herbivory rates across different seasons may not be strongly related to single leaf trait. Evidently, dominant leaf traits and foliar herbivore interactions in tropical dry evergreen forest are highly specific and also further influenced by season. In our results, leaf damage was high for those plant species with high specific leaf area (SLA) and this agrees with the prediction of Poorter *et al*. (2004) that trees with low SLA would host lesser number of herbivores. Thus, insect abundance and leaf damage are dependent on the resource availability and quality such as palatability and total biomass content, to meet the dietary need of foliar herbivores. The most dominant species of TDEF (Parthasarathy *et al*. 2008) exhibit maximum foliar damage in wet season (pre-monsoon and monsoon) and this subscribes for the significant relation obtained between foliar herbivory and plant density, but in dry season, the pattern differs. This result also corroborates with the findings of other studies (Janzen 1970, Barone 1998, Angulo-Sandoval & Aide 2000) explaining the higher rate of herbivory in plant species occurring in higher densities. In monsoon season the numbers of foliar herbivores are high and they seem to exploit the most dominant favourable leaf traits that prevail in TDEF species such as coriaceous and sub-coriaceous texture and glabrous leaves. In dry season (post-monsoon and summer), foliar herbivores of TDEF mainly depend on leaf biomass, because microphyll leaves are dominant leaf size in our study, but mesophyll leaves exhibit maximum leaf damage in these seasons. The positive relationship obtained between specific leaf area (SLA) and leaf damage also supports this view point. Admittedly, foliar herbivory and leaf damage in TDEF are governed by various leaf traits, seasons and plant density as well.

CONCLUSIONS

This study investigated the leaf traits and leaf resource use by faunal community in the under-studied tropical dry evergreen forest (TDEF) of India and revealed the degree of specialisation between foliar herbivores and individual leaf traits of this unique forest type, which are further influenced by seasonal variation, plant density and herbivore abundance. The tropical dry evergreen forest supports a rich herbivore fauna of beetles, lepidopteran larvae and grasshoppers and many of which help in ecosystem functioning of the TDEF. This study underlines the importance of community-level approach in plant resource use by faunal communities for better understanding of the forest biotic interactions useful for conservation.

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Appendix I. Leaf traits, foliar herbivores and per cent leaf damage of 110 plant species of tropical dry evergreen forest on the Coromandel Coast of India.

Plant species	Family	SS	PT	LT	LR	LS	LA	SLA	FH	Per cent leaf damage (Mean± Sd)			
										Monsoon	Post-monsoon	Summer	Pre-monsoon
Trees													
Aglaia elaeagnoidea (Juss.) Benth.	Meliaceae	4	E	C	Co	G	Mi	105.31	L1	20±1.4	2.3±0.7	0.8±0.07	16.5±1.4
Albizia amara (Roxb.) Boivin	Mimosaceae	10	D	Cpi	M	G	Na	110	L9	22.8±0.4	1.4±0.2	0.6±0.07	14±1.4
Albizia lebbeck (L.) Benth.	Mimosaceae	4	D	Cpi	M	G	Mi	63.13	L29	17.5±2.1	0.4±0.1	0.8±0.07	12.5±0.7
Allophyllus serratus (Roxb.) Kurz	Sapindaceae	4	E	Ctri	Sco	G	Mi	137.36	L16	15.5±0.7	2.9±0.3	0.7±0.07	12.5±1.4
Atalantia monophylla (L.) Correa	Rutaceae	10	E	S	Co	G	No	459.43	L32, L37	36.3±6.7	4±0.4	2.9±0.71	22±1.4
Azadirachta indica A. Juss.	Meliaceae	10	B	C	Sco	G	Mi	234.43	L18	29.5±0.7	.2±0.1	0.8±0.14	16.5±0.7
Barringtonia acutangula (L.) Gaertner	Barringtoniaceae	4	E	S	Sco	G	Me	71.76	L20	5±0.7	13.5±1.5	3.6±0.71	3.6±0.1
Bauhinia racemosa Lam.	Caesalpiniaceae	4	D	S	Sco	E	Mi	97.92	L21	4.5±2.1	18.3±1.4	4.5±0.35	2.7±0.2
Benkara malabarica (Lam.) Tirven.	Rubiaceae	4	E	S	Co	E	Mi	42.47	L5	13.3±2.5	17.3±0.0	1.3±0.07	6.8±1.1
Breynia vitis-idaea (Burm. f.) Fischer	Euphorbiaceae	4	E	S	M	G	Mi	32.61	Bt2	7.4±1.3	13.8±1.0	4.7±0.71	4±0.7
Butea monosperma (Lam.) Taubert	Papilionaceae	4	D	Ctri	Co	G	Me	106.26	L29	24±0.7	16.1±0.0	2.6±0.28	15±0.7
Calophyllum inophyllum L.	Clusiaceae	4	E	S	Co	G	Me	115	Bt2	20.9±2.0	12.3±0.0	6.5±0.71	8.5±1.4
Canthium dicoccum (Gaertn.) Teijsm. & Binn.	Rubiaceae	10	E	S	Co	G	No	141.94	L8, L34	40.2±1.7	8.2±1.3	3.9±0.71	23±2.1
Cassia fistula L.	Caesalpiniaceae	4	D	Cpi	Sco	G	No	255.59	L3	23.3±1.1	12.8±0.5	7.3±0.71	17±0.7
Chionanthus zeylanica L.	Oleaceae	10	E	S	Co	G	Mi	58.54	L2	14.5±0.7	13.6±0.6	5.6±0.42	9±0.7
Cordia obliqua Willd.	Cordiaceae	4	B	S	Co	G	Mi	116.67	L21	30.3±1.2	11.4±1.3	3.6±0.21	15.7±0.4
Crateva magna (Lour.) DC.	Capparaceae	4	D	Ct	M	G	Me	219.35	Bt3	16.5±1.4	9.7±0.6	4.6±0.33	11.9±1.3
Diospyros ebenum Koen.	Ebenaceae	10	E	S	Co	G	No	75.57	L19	21.9±0.6	4±0.3	1.6±0.71	12.7±1.0
Diospyros ferrea (Willd.) Bakh.	Ebenaceae	4	E	S	Co	G	Mi	89.17	L19	11±0.7	2.8±0.8	0.3±0.14	6.7±0.5
Drypetes sepiaria (Wight & Arn.) Pax & Hoffm..	Euphorbiaceae	4	E	S	Co	G	Mi	92.12	Bt2, L35	37±1.4	2.3±1.2	0.6±0.07	19.1±0.5
Ehretia pubescens Benth.	Boraginaceae	4	B	S	Sco	Hp	Mi	76	Bt1	17.8±1.9	2.8±0.7	0.3±0.07	13±0.7
Eugenia bracteata (Willd.) Roxb.	Myrtaceae	4	E	S	Co	Hs	Me	70.46	Bt4	4±1.4	11.2±1.4	0.5±0.07	2.6±0.1
Ficus benghalensis L.	Moraceae	4	B	S	Co	Hs	Me	75.48	Bt3	18±1.4	13.3±1.6	4.5±0.42	9±0.7
Ficus hispida L. f.	Moraceae	4	B	S	Co	Hh	Me	83.15	L26	14.0±0.8	19.2±2.7	6.7±0.07	8.5±1.4
Ficus religiosa L.	Moraceae	4	B	S	Co	G	Me	105.22	Bt1	26±1.4	8.2±1.3	4.5±0.07	16.7±0.4

Flacourtia indica (Burm. f.) Merr.	Flacourtiaceae	4	B	S	Ch	G	Mi	280.5	Bt2	25±2.8	10.7±2.1	3.5±0.42	13.6±0.6
Garcinia spicata (Wight & Arn.) J.D. Hook.	Clusiaceae	4	E	S	Co	G	Me	79.89	Bt1	17±1.4	11.2±1.3	4.8±0.71	8.5±1.4
Glycosmis mauritiana Yuich. Tanaka	Rutaceae	4	E	S	Sco	G	Mi	126.15	L32, L37, Bt8	25.3±5.9	2±0.4	1.1±0.14	16.5±1.4
Gmelina asiatica L.	Verbenaceae	4	E	S	M	G	Mi	18.97	Bt4	12±0.7	2.7±0.7	1.5±0.25	6±0.7
Ixora pavetta T. Anderson	Rubiaceae	4	E	S	Co	G	No	97.92	L15	16±2.8	2.7±0.1	0.5±0.14	8±0.7
Lannea coromandelica (Houtt.) Merr.	Anacardiaceae	4	D	Cpi	Sco	G	No	101.14	Bt2	32±0.7	3.7±0.1	1.3±0.48	17±
Lepisanthes tetraphylla (Vahl.) Radlk.	Sapindaceae	10	E	Cpi	Sco	G	Me	47.63	L1, L6, W2	36±2.1	9.4±0.2	4.7±0.7	22±0.7
Mallotus philippensis (Lam.) Muell.-Arg.	Euphorbiaceae	4	E	S	Sco	G	Me	65	Bt3	12.1±2.9	7.7±0.7	4.4±0.44	7.5±0.7
Mallotus rhamnifolius Muell.-Arg.	Euphorbiaceae	4	E	S	Ch	G	Me	64.63	Bt2	7.5±1.4	9.4±0.1	1.2±0.07	5.8±0.4
Manilkara hexandra (Roxb.) Dubard	Sapotaceae	4	B	S	Co	G	No	54.84	Bt3	13.5±2.8	4.1±0.7	1.6±0.14	6.5±1.4
Maytenus emarginata (Wild.) Ding Hou.	Celastraceae	4	E	S	Co	G	Mi	51.37	Bt4	14±1.4	1.4±0.2	0.3±0.07	7.65±0.2
Memecylon umbellatum Burm. f.	Melastomataceae	10	E	S	Co	G	Mi	60.71	L23, L24, L33	43±0.7	1.4±0.1	0.4±0.03	39±7.1
Mimusops elengi L.	Sapotaceae	4	E	S	Co	G	No	85.16	L2	12.5±1.4	3.6±0.1	1.6±0.21	7±0.7
Morinda coreia Buch. -Ham.	Rubiaceae	10	E	S	Co	G	No	217.69	L8	31.6±2.3	4.6±0.3	2.2±0.07	15.8±0.4
Morinda pubescesns Sm.	Rubiaceae	4	B	S	Co	H	No	265.93	Bt1	31.8±1.1	5±0.2	1.3±0.14	15.5±2.1
Ochna obtusata DC.	Ochnaceae	4	D	S	Co	G	No	94.64	Bt4	21.3±1.8	3.6±0.2	1.3±0.07	13±0.7
Pamburus missionis (Wight) Swingle	Rutaceae	4	E	S	Co	G	No	62.28	L11	7±0.7	6.4±0.1	3.3±0.71	5.5±4.2
Pleiospermium alatum (Wall. ex Wight. & Arn.) Swingle	Rutaceae	4	E	S	Co	G	No	241.62	Bt2	18.6±0.5	3.4±0.3	1.4±0.07	12.5±1.4
Pongamia pinnata (L.) Pierre	Papilionaceae	4	B	Cpi	Sco	G	Mi	55.26	Bt3	24±2.1	3.3±0.7	0.5±0.02	14±1.4
Premna latifolia Roxb.	Verbenaceae	4	E	S	Sco	H	Mi	26.55	Bt4	15.5±1.4	2.6±0.2	1.4±0.42	6.5±0.7
Pterospermum canescens Roxb.	Sterculiaceae	10	B	S	Co	G	Mi	86.11	Bt5	32.5±1.4	1.8±0.0	0.2±0.07	18±1.4
Pterospermum xylocarpum (Gaertn.) Sant. & Wagh.	Sterculiaceae	4	B	S	Co	G	No	83.56	Bt6	31.5±1.4	3.6±0.3	1.5±0.07	18±2.8
Salvadora persica L.	Salvadoraceae	4	B	S	Co	G	Mi	68.94	Bt2	6.8±1.1	1.9±0.1	1.4±0.07	2±0.7
Sapindus emarginatus Vahl	Sapindaceae	4	B	Cpi	Sco	G	Mi	54.47	Bt4	12±0.7	2.7±0.1	1.5±0.04	6.9±1.2
Securenega leucopyrus (Willd.) Muell.-Arg.	Euphorbiaceae	4	E	S	M	G	Na	16.11	Bt7	5.5±1.4	1.1±0.5	0.3±0.02	3.5±1.4
Semecarpus anacardium L. f.	Anacardiaceae	4	D	S	Co	G	No	6.46	Bt2	3.8±1.1	3.3±0.0	0.7±0.07	0.8±0.1
Streblus asper Lour.	Moraceae	4	E	S	Sco	Hs	Mi	96.58	Bt3	4.2±1.2	2.4±0.1	0.9±0.07	4±0.7
Strychnos nux-vomica L.	Loganiaceae	4	D	S	Sco	G	No	78.33	Bt4	5.8±0.4	4.9±0.1	2.1±0.07	3.3±0.4

Syzygium cumini (L.) Skeels	Myrtaceae	4	B	S	Co	G	Me	145.68	Bt5	24±2.1	6.5±1.4	3.3±0.07	15.4±0.9
Tamarindus indica L.	Caesalpiniaceae	4	B	Cpi	M	G	Na	62.5	Bt6	2.9±0.2	3.5±0.2	1.1±0.14	0.9±0.2
Tarenna asiatica (L.) Kuntz ex Schumann	Rubiaceae	4	E	S	Co	G	No	53.67	L14	10.8±1.1	4.7±0.1	2.2±0.08	9±2.8
Terminalia bellirica (Gaertn.) Roxb.	Combretaceae	4	D	S	Co	G	Me	69.55	GH1, L6	2.8±1.1	8.7±0.1	3.8±0.07	1.7±0.3
Tricalysia sphaerocarpa (Dalz.) Gamble	Rubiaceae	10	E	S	Sco	G	No	33.11	Bt7	22±0.7	3.8±0.0	1.7±0.14	14.5±4.2
Vitex altisima L. f.	Verbenaceae	4	D	Ctri	Sco	G	Mi	19.58	GH3	5±0.7	2.4±0.0	1.2±0.07	2±0.7
Walsura trifolia (A.Juss.) Harms	Meliaceae	4	E	Ctri	Co	G	No	88.64	L10, L30	17±0.7	3.8±0.0	1.4±0.02	11.6±0.6
Lianas													
Abrus precatorius L.	Papilionaceae	4	B	Cpi	M	Hp	Na	23.43	GH2	2±0.7	0.2±0.0	0.2±0.02	7.5±8.5
Acacia caesia (L.) Willd.	Mimosaceae	10	B	Cpi	M	G	Mi	18.87	Bt5	2.7±0.5	1.2±0.0	0.3±0.07	3.4±1.3
Ampelocissus tomentosa (Heyne ex Roth) Planch.	Vitaceae	2	B	Cpal	Sco	H	Me	134.3	Bt2	12.8±0.4	8.5±0.0	2.8±0.21	6.8±0.3
Argyreia cymosa (Roxb.) Sweet	Convolvulaceae	4	E	S	Sco	G	No	46.13	Bt3	2.7±0.4	3.5±0.2	1.3±0.03	1.8±0.4
Canavalia virosa (Roxb.) Wight & Arn.	Papilionaceae	4	D	Ctri	Sco	G	Mi	28.67	Bt4	5.8±0.4	2.2±0.1	1.3±0.09	2.6±0.6
Cansjera rheedii Gmel.	Opiliaceae	4	E	S	Co	G	No	76.08	Bt5	3.7±0.5	3.6±0.1	1.4±0.07	1.7±0.3
Capparis brevispina DC.	Capparaceae	10	E	S	Sco	G	No	90.63	Bt6	13.3±1.8	2.8±0.1	1.2±0.02	7.6±0.1
Capparis rotundifolia Rottl.	Capparaceae	4	E	S	Sco	G	Mi	79.29	Bt3	14.5±1.4	5±0.7	1.7±0.21	3.6±0.1
Capparis sepiaria L.	Capparaceae	4	E	S	Sco	G	Mi	43.13	Bt1	10.3±0.4	1.7±0.1	0.5±0.14	5.4±0.1
Capparis zeylanica L.	Capparaceae	4	E	S	Sco	G	No	171.37	Bt3	18.5±1.4	4.6±0.2	2.4±0.21	13.3±0.4
Carissa spinarum L.	Apocynaceae	10	E	S	Co	G	Mi	30.47	Bt6	4±0.7	2.4±0.2	2.2±0.07	1.5±0.1
Cayratia pedata (Lam.) Juss. ex Gagnep.	Vitaceae	4	E	Cpal	Sco	H	Mi	106.22	Bt9	33.8±1.1	2.6±0.2	1.1±0.14	15.6±1.3
Cissampelos pareira L. var. *hirsuta* (Buch.-Ham. ex DC.) Forman	Menispermaceae	4	B	S	Sco	H	No	304.59	L3	21.2±1.7	2.5±0.0	1.3±0.07	12.1±0.6
Cissus quadrangularis L.	Vitaceae	10	E	S	Co	G	Mi	20.14	L2	2.1±0.9	3.5±0.3	1.5±0.07	0.8±0.0
Cissus vitiginea L.	Vitaceae	10	D	S	Co	H	No	230.72	L5	27±2.1	6.5±0.4	2.5±0.07	17.8±2.5
Coccinia grandis (L.) Voigt	Cucurbitaceae	10	E	S	Sco	G	Mi	11.27	Gh3, L6	2.7±0.2	2.8±0.7	0.6±0.07	1.5±0.0
Combretum albidum G.Don	Combretaceae	10	D	S	Sco	G	Me	198	GH1, L7	34.5±3.5	8.8±0.1	1.6±0.14	13.9±2.3
Derris ovalifolia (Wight & Arn.) Benth.	Papilionaceae	4	E	Cpi	Sco	G	Mi	25	Bt4, Gh2	2.5±0.7	3.2±1.4	1.8±0.07	1.7±0.3
Dioscorea oppositifolia L.	Dioscoreaceae	4	D	S	M	G	No	262.85	Gh4	21.5±1.4	4.5±0.4	2.4±0.07	16.9±0.9

Grewia rhamnifolia Heyne ex Roth	Tiliaceae	10	B	S	Sco	H	No	182.42	L4	32.5±2.8	3.9±0.1	1.3±0.14	15.4±0.1
Gymnema sylvestre (Retz.) R.Br. ex Schultes	Asclepiadaceae	10	E	S	Sco	G	Mi	26.79	L31	8.5±1.4	1.6±0.5	0.5±0.07	7.1±0.9
Hugonia mystax L.	Linaceae	10	E	S	Ch	G	Mi	9.15	L4	2.5±1.4	5.4±0.7	2.4±0.07	0.7±0.1
Ichnocarpus frutescens (L.) R.Br.	Apocynaceae	4	E	S	Co	G	Mi	5.08	L12	4.2±1.7	10.5±0.4	4.7±0.07	1.5±0.1
Jasminum angustifolium (L.) Willd.	Oleaceae	4	E	S	Co	G	Mi	121.88	L30	12.5±2.1	1.6±0.4	0.8±0.07	2.9±0.1
Lantana camara L.	Verbenaceae	4	E	S	Sco	H	No	57.43	L21, Gh5	12.5±1.4	7.6±0.4	1.6±0.05	12.6±0.9
Leptadenia reticulata (Retz.) Wight & Arn.	Asclepiadaceae	4	B	S	Co	G	Mi	11.94	L38, Bt7	5.7±0.5	2.5±0.5	1.3±0.07	2.5±0.7
Maerua oblongifolia (Forsk.) A.Rich.	Capparaceae	4	E	S	Sco	G	Mi	19.79	Bt1	2.5±0.7	2.6±0.7	1.3±0.07	2.5±1.4
Mukia maderaspatana (L.) M. Roem.	Cucurbitaceae	4	B	S	Sco	Hs	Mi	189	Bt4	10.5±1.4	1.3±0.7	0.4±0.27	5.5±1.4
Olax scandens Roxb.	Olacaceae	4	E	S	Co	H	Mi	10.07	Bt3	3±0.7	2.9±0.1	1.5±0.07	2.7±0.2
Pachygone ovata (Poir) Miers ex Hook.	Menispermaceae	10	E	S	Co	G	No	215.63	Bt3	27.5±2.1	3.8±0.1	1.7±0.14	17.5±0.7
Plecospermum spinosum Trecul	Moraceae	4	E	S	Co	G	No	165.85	Bt5	19±0.7	3±0.7	1.2±0.05	14±2.8
Premna corymbosa (Burm.f.) Rottl. & Willd.	Verbenaceae	10	E	S	Sco	G	No	423.2	Bt6	11±0.7	2.4±0.1	1.5±0.14	4.3±1.1
Pyrenacantha volubilis Wight	Icacinaceae	10	E	S	Sco	G	Mi	151.6	Bt7	23.5±1.4	8.7±0.7	4.4±0.49	10±1.4
Reissantia indica (Willd.) Halle	Celastraceae	10	E	S	Sco	G	Mi	22.66	Bt5	26.5±1.4	5.5±0.5	2.6±0.28	20.5±1.4
Rivea hypocrateriformis (Desr.) Choisy	Convolvulaceae	4	E	S	Co	G	Mi	100	Bt6	31.5±0.7	3.6±0.2	1.4±0.14	15±2.8
Salacia chinensis L.	Hippocrateaceae	4	E	S	Sco	G	Mi	105	Bt1	22.5±0.7	2.5±0.5	1.5±0.14	14.5±0.7
Strychnos lenticellata Hill	Loganiaceae	10	E	S	Co	G	Mi	64.3	Bt4	23±2.1	2.4±0.1	1.4±0.07	16.5±1.4
Tiliacora acuminata (Lam.) Hook. f. & Thoms.	Menispermaceae	4	E	S	Sco	G	No	31.69	Bt2	10.7±1.0	2.8±0.1	1.3±0.07	7±1.4
Tinospora cordifolia (Willd.) Hook. f. & Thoms.	Menispermaceae	4	D	S	Sco	G	Mi	27.05	Bt3	28.5±1.4	2.6±0.4	1.2±0.14	14.5±3.5
Toddalia asiatica (L.) Lam.	Rutaceae	4	E	Ctri	Sco	G	Mi	10.12	L12	21±1.4	3.8±0.1	1.8±0.12	8.5±1.4
Toxocarpus kleinii Wight & Arn.	Asclepiadaceae	4	E	S	M	G	No	43.43	L3	3.5±0.7	3.4±0.1	1.5±0.52	2±0.7
Tylophora indica (Burm. f.) Merr.	Asclepiadaceae	4	D	S	co	G	Mi	127	L36	11±1.4	6.5±0.1	2.5±0.31	3.6±0.6
Ventilago madraspatana Gaertn.	Rhamnaceae	4	E	S	Sco	G	Mi	15.39	Bt5	13±1.4	7.5±0.0	3.5±0.64	4±0.7
Wattakakka volubalis T. Cooke	Asclepiadaceae	4	E	S	M	G	No	102.89	L3	23.5±1.4	4.6±0.4	3.4±0.29	19±2.8
Zizyphus oenoplia (L.) Mill.	Rhamnaceae	10	B	S	Sco	H	Mi	93.63	L28, L31	24.5±0.7	3.5±0.0	1.5±0.07	17±2.1

Herbs												
Dendrophthoe falcata (L. f.) Ettingsh	Loranthaceae	4	E	S	Co	G	Mi	Bt2	13.4±1.6	6.8±0.4	0.8±0.35	11.3±1.4
Ecbolium viride (Forssk.) Alston	Acanthaceae	4	E	S	Sco	H	Mi	L39	3.9±0.7	1.9±0.3	1.4±0.21	1.8±0.4
Phoenix pusilla Gaertn.	Arecaceae	4	E	S	Co	G	Mi	Bt1	7±2.1	2.9±0.9	0.8±0.35	5.5±1.1
Sanseveria roxburghii Schultes & Schultes	Agavaceae	10	E	S	Suc	G	No	Gh2	7±0.7	1.2±0.1	0.9±0.49	4.8±0.6
Theriophonum minutum (Willd.) Baillon	Araceae	4	E	S	Sco	G	Mi	Gh1, Bt1	7.5±1.0	1.9±0.5	1.1±0.14	3.8±0.4

Note: SS (Sample size): 30 leaf samples from each individuals of 10 plants for dominant species, 4 for sub-dominant and 2 for rare species. PT (Plant type): E = Evergreen; B = Brevi-deciduous; D = Deciduous; LF (Life-form): T = Tree; L = Liana; H = Herb. LT (leaf type): S = simple; C = compound. LR (Leaf texture): M = membranous; Ch = chartaceous; Co = coriaceous; Sco = sub coriaceous; LS (Leaf surface): G = Glabrous; H = Hairy (Hp = Pubescent; Hs = Scabrid, Hh = Hispid); LA (Leaf area): Nanophyll (0.25-2.25 cm^2); Microphyll (2.25-20.25 cm^2); Notophyll (20.25-45 cm^2); Mesophyll (45-182.25 cm^2); SLA (Specific leaf area); FH (Foliar herbivores): B = Beetle; W = Weevil; L = Larvae (Lepidoptera); Gh = Grasshopper; For expansion of codes see Supplementary table II); For per cent leaf damage data of two years were averaged for each season.